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STUDIORUM PROGRESSUS

The Colour Change of the Zoea of the Shrimp, *Crangon crangon* L.

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Introduction.—It was in the middle of the nineteenth century that zoologists detected in some decapod crustaceans the existence of integumentary chromatophores, as well as the physiological colour change produced by their activity. But the first detailed description of the chromatic activity in shrimps and prawns was given by POUCHET[2], whose observations in this field were later developed by KEEBLE and GAMBLE[3] and by MINKIEWICZ[4]. On the basis of the results obtained by these older investigators the conclusion can be drawn that some shrimps and prawns possess the capacity of adapting themselves to the coloration of the background.

A next step, and a very important one in the research work on crustacean colour change, was made by KOLLER[5], who detected that this process is regulated by hormones present in the circulating blood. PERKINS[6], using different methods and working independently, confirmed KOLLER's statement. HANSTRÖM[7] was able to identify the sinus gland of the decapod eye-stalk as a source of chromatophorotropic hormones. According to the present state of knowledge, HANSTRÖM's sinus gland is the most important incretory organ of higher crustaceans, but not the only one. BROWN and his collaborators[8] showed in a series of investigations that chromatophorotropic hormones in decapods can be produced also in some parts of the central nervous system, and especially in the tritocerebral commissures.

The colour change of the shrimp, *Crangon crangon* L., was studied in detail by KOLLER[9]. *Crangon* has a sense of colour; the animal distinguishes blue from yellow, orange and red, but not from green. This rather well-developed colour sense gives the shrimp a very fine adaptation to backgrounds as diverse in colour as white, yellow, orange, red and black. This ability of the animal to harmonize its colour with its environment may be of protective value under natural life conditions.

The structure of the chromatophoral system of the adult shrimp, *Crangon*, is one of the most complex known among the crustaceans. The description of KOLLER contained a list of 4 different pigments (sepia-brown, white, yellow and red), but according to the later observations of BROWN and WULFF[1], KOLLER's sepia-brown should be differentiated into a brown and a black pigment. These 5 pigments may appear separately in monochromatic cells or form combinations of bi-, tri- and tetrachromatic chromatophores. The particular types of pigmentary cells constitute groups characteristic of definite regions of the shrimp's body. The complexity of this pattern is further increased by the fact that the chromatophores of the respective body regions may show different physiological properties.

It is known that the animal tends to adapt itself to the colour of the bottom by a kind of neurohumoral reflex. This is brought about in the following manner: once the compound eye has been affected by light, the stimulus is conveyed through the central nervous system to the sinus gland or some neurosecretory centre. The response thus created produces in the gland or the neurosecretory cells a number of hormones which may change the state of the chromatophores. This rather simple scheme of reaction does not give a full explanation for all the manifestations of chromatic adaptation in *Crangon*. In fact the investigations in this field are still faced with a number of unsolved problems. But it has been proved that a very important factor in these reactions is the ratio of light reflected from the background to the incident light (albedo).

The chromatophoral system of the zoea (first larval stage) of *Crangon* is not as complex as that of the adult forms. The chromatophores included in it are few in number and show fairly regular distribution. It contains blackish brown monochromatic pigmentary cells, as well as the less numerous bichromatic ones provided with brown and yellow pigment. As it develops further, this system of chromatophores, from being a primary one (KEEBLE and GAMBLE[2]), evolves into a more complex and irregular secondary chromatophoral system typical of the adult shrimp.

Experimental results and discussion.—By studying the zoea's chromatophores under different conditions, it was found that their responses differ essentially from those shown by the chromatophores of the adult shrimp. The reflected light is a non-contributory factor, as only the incident rays are instrumental in producing the colour change. This has been proved by a series of experiments in which the zoeas were placed in 3 different kinds of surroundings, which were: (1) a white-walled container, exposed to sun-light, (2) a black-walled container, subject to similar illumination, and (3) a container placed in the dark-room. Each container received a series of 5 zoeas, which remained in the conditions mentioned on August 19th, 1951, from 10 a.m. to 11[30] a.m. (insolation intensity 0·49 cal. g/cm^2, air temperature 20–35°). All the larvae in the illuminated containers (white-walled and black-walled) reacted by pigment dispersion in the chromatophores and those placed in the dark-room by pigment concentration. Both kinds of pigment were involved in these changes. In this type of colour change the albedo does not appear to play any part whatever, and there is also no adaptation to the background. This conclusion does not conform with the earlier view of KOLLER[3]. This

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[2] G. POUCHET, J. Anat. Physiol. *8*, 401 (1872); *9*, 290 (1873); *12*, 1 und 113 (1876).

[3] F. KEEBLE and F. W. GAMBLE, Proc. Roy. Soc. London [B] *65*, 461 (1900); *71*, 69 (1903); Philosoph. Transact. Roy. Soc. London [B] *196*, 295 (1904); *198*, 1 (1905).

[4] R. MINKIEWICZ, Bull. Acad. Sci. Cracovie *1908*, 918.

[5] G. KOLLER, Verh. dtsch. Zool. Ges. *30*, 128 (1925); Z. vgl. Physiol. *8*, 601 (1928).

[6] E. B. PERKINS, J. exp. Zool. *50*, 71 (1928).

[7] B. HANSTRÖM, Kungl. Svenska Vetenskap. Handl. *16*, 1 (1937).

[8] F. A. BROWN, Jr., Physiol. Zool. *19*, 215 (1946). – F. A. BROWN, Jr., and H. E. EDERSTROM, J. exp. Zool. *85*, 53 (1940). – F. A. BROWN, Jr., and A. MEGLITSCH, Biol. Bull. *79*, 409 (1940). – F. A. BROWN, Jr., and V. J. WULFF, J. Cell. comp. Physiol. *18*, 339 (1941).

[9] G. KOLLER, Z. vgl. Physiol. *5*, 191 (1927); *12*, 632 (1930).

[1] F. A. BROWN, Jr., and V. J. WULFF, J. Cell. comp. Physiol. *18*, 339 (1941).

[2] F. KEEBLE and F. W. GAMBLE, Philosoph. Transact. Roy. Soc. London [B] *196*, 295 (1904).

[3] G. KOLLER, Z. vgl. Physiol. *5*, 191 (1927).

author writes that "... die Larven... in dunkler Umgebung eine weitgehende Expansion der Pigmente zeigten. Nach Verbringung in helle Umgebung erfolgte deutliche Kontraktion." Evidently KOLLER did not see the difference in the chromatic behaviour of the larvae and that of the adults; this is certainly incorrect.

Further experiments revealed that the effects produced in the chromatophores not only depend on the intensity of light but also on its wave-length. This was proved by transfering the larvae into white-walled containers exposed to sun-light which was passed through 3 different glass filters. These were: (1) an ultraviolet-violet filter (wave-length 300–450 mμ), (2) a blue one (wave-length 450–500 mμ) and a red one (wave-length about 660 mμ)[1]. Each container received a series of 6 larvae. After the animals had been irradiated for 1 h (August 19th, 1951, from 14 p.m. to 15 p.m., insolation intensity 0·36 cal.g/cm^2, air temperature 23°), the state of the chromatophores of the three groups was registered with the following results: (1) a very pronounced pigment dispersion was noted under the ultraviolet filter, (2) a lesser degree of dispersion under the blue filter, and (3) a pigment concentration under the red one. The conclusion to be drawn is that, as regards the zoea's chromatophores, the short-waved rays, and particularly the ultraviolet ones, induce pigment dispersion which produces the effect of darkening of the external coloration, whereas long-waved light tends to produce the concentration of pigment and subsequent paling of the animal. It should also be mentioned here that the results given above stand in no relation to the varying values of intensity of the rays passed through the different filters. The intensity of sunlight passed through the three filters was measured by a thermoelectric solarimetre (the GORCZYNSKI type). The red filter showed the highest intensity value, the blue filter an intermediate one, the ultraviolet-violet filter giving the lowest intensity of the 3 tested glasses. The energy of the filtered light diminishes inversely to the decrease of the pigment dispersion (from long to short waves in the first case and from short to long waves in the second case).

It was also found that the immersion of larvae in an aqueous solution of the sinus gland hormones of an adult shrimp had no effect whatever upon the chromatophores. For this type of experiment, a total number of 16 larvae was used. The chemical colour change agents of the adult animal are evidently inactive in the case of the zoea.

The character of changes observed in the experiments mentioned above seems to indicate that the action of light on the chromatophores is, in this case, a direct one. The behaviour of the chromatophores of the zoea of *Crangon* resembles the type of reaction seen in blinded decapods (KLEINHOLZ and WELSH[2]) and blinded isopods (SMITH[3], SUNESON[4]) in the mature stage. In animals from these crustaceans groups, in which the neurohumoral colour change mechanism with the compound eye as receptor is experimentally eliminated, the chromatophores react to illumination by pigment dispersion, caused by direct stimulation of these cells by the rays.

[1] The differences of temperature which could possibly arise in the containers as the consequence of the different transmittance of the filters used, were eliminated by a cooling arrangement which maintained the water temperature on a level approximatively equal to that of the air.

[2] L. H. KLEINHOLZ and J. H. WELSH, Nature, London *140*, 851 (1937).

[3] H. G. SMITH, Proc. Roy. Soc. London [B] *125*, 250 (1938).

[4] S. SUNESON, Kungl. Fysogr. Sällsk. Handl. *58*, 1 (1947).

But it has also been proved by many authors (initially by BABÁK[1]) that the early larval forms of vertebrates

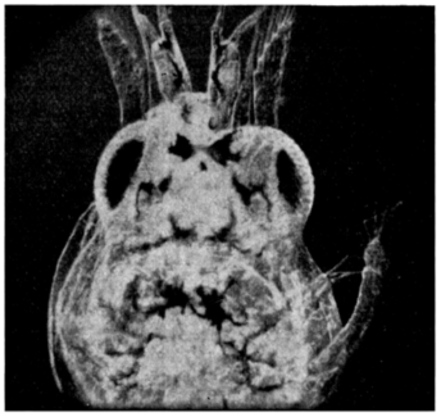

Fig. 1.—The effect of darkness on the chromatophores of the shrimp's zoea: concentration of the pigment.

Fig. 2.—The effect of insolation through a blue filter on the chromatophores of the shrimp's zoea: the pigment in the cells less concentrated than that in Figure 1.

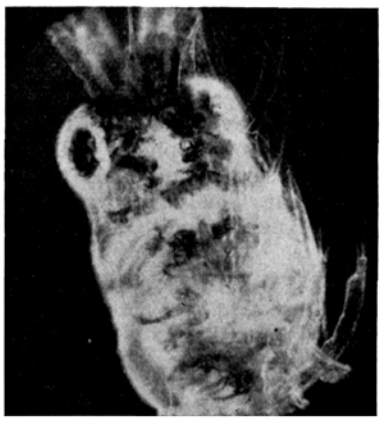

Fig. 3.—The effect of insolation whithout filter on the chromatophores of the shrimp's zoea: dispersion of the pigment.

may show a similar type of chromatophoral reactions. The larvae of many fishes and amphibians react to illumination by melanin dispersion in the chromatophores

[1] E. BABÀK, Pflügers Arch. *131*, 87 (1910).

and by melanin concentration in same if placed in the darkness. In later stages of development, this primary type of colour response is replaced by a secondary type of response, which consists in the main in a background adaptation. Here the differences can possibly be explained by the respective significance of the chromatophoral system in the life of the larvae and in that of the adults. In the latter, the colour change makes it possible to effect concealment through background adaptation; in the larvae, the activity of chromatophores may lead to protection of internal organs against the harmful effect of light.

This evidently also holds true of the zoea of *Crangon*. In contrast to the adults, the larvae have a planktonic mode of life and float in the superficial water layers, being exposed to an intensive solar irradiation. In this connection it may be interesting to note that their chromatophores are located very closely to the chief internal organs, especially to the nervous system (see the big paired chromatophores between the eyes, Fig. 1 and Fig. 2).

Unfortunately, it was not possible, in my experiments, to observe the metamorphosis of the *Crangon's* zoea into the subsequent larval stages, and for the same reason no observations could be made at which point of development the primary colour response is replaced by the secondary one. It seems rather probable, however, that in settling this question, a comparative consideration of the properties of the chromatophores in other crustacean groups might prove useful.

It is well known that the decapod larvae, the zoea and even more the following mysis stage show a striking resemblance to the adult forms of the *Mysidae*. That also holds true of the chromatophoral system of the shrimp's zoea. It has been proved by KOLLER and MEYER[1] and later by CHICEWICZ[2] that in the *Mysidae* there is a neurohumoral regulation of the chromatophores, comparable to that of the decapods. But CHICEWICZ found also that the pigmentary cells of the mysid species *Praunus flexuosus* can to a certain degree be stimulated directly by light.

Taking for granted that the morphological resemblance of the decapod larvae and the *Mysidae* justifies our making some assumptions as to the existence of common phylogenetic stages in the development of the chromatophoral system, it seems probable that the primary type of response is replaced by the secondary one before the former has developed into the latter. According to this theory, *Praunus* represents the stage in which the response has already developed into the secondary type but the system of chromatophores still persists on the primary level. The same is probably true of the ontogenetic development. This can be presumed from the observations of KEEBLE and GAMBLE[3], according to which the decapod larvae show signs of background reaction at the moment at which the eye-stalks grow out.

In this way, the following stages can be assumed to exist in the ontogenetic and phylogenetic development of the chromatophoral system in higher crustaceans and in the types of reactions:

	System	Type of response
1st stage (decapod zoea) . .	primary	primary
2nd stage (*Praunus*)	primary	secondary
3rd stage (adult decapods) .	secondary	secondary

[1] G. KOLLER and E. MEYER, Biol. Zbl. *50*, 759 (1930).

[2] M. CHICEWICZ, Bull. Acad. Sci. Cracovie [B] *II* (1951), in print.

[3] F. KEEBLE and F. W. GAMBLE, Philosoph. Transact. Roy. Soc. London [B] *196*, 295 (1904).

Zusammenfassung

Das Chromatophorensystem der Zoëa-Larve der Sandgarnele *Crangon crangon* L. ist einfacher ausgebildet als das der erwachsenen Garnele und zeigt auch ein anderes Verhalten Lichtreizen gegenüber. Dieses sogenannte primäre Chromatophorensystem reagiert nur auf einfallendes Licht, und zwar durch Pigmentdispersion, wobei kurzwelliges Licht mehr aktiv ist. Das sekundäre Chromatophorensystem der erwachsenen Garnele dagegen zeigt Anpassung an den Untergrund, wobei der jeweilige Zustand der Farbzelle abhängig ist von dem Verhältnis: reflektiertes Licht: einfallendes Licht (Albedo).

Der Farbwechsel des sekundären Systems ist bekanntlich von einem neurohumoralen Reflex mit Einschluss der endokrinen Tätigkeit der Sinusdrüse abhängig, in dem primären System dagegen scheint eine direkte Reizung der Chromatophoren durch Lichtstimuli stattzufinden.

Ein Vergleich mit dem Farbwechsel der *Mysidae* erlaubt zu vermuten, dass auch in der phylogenetischen Entwicklung des Chromatophorensystems der höheren Kruster ähnliche Stadien aufeinanderfolgten.

CONGRESSUS

Suisse

XIe Congrès ornithologique international

Le XIe Congrès ornithologique international, présidé par Sir LANDSBOROUGH THOMSON, Londres, aura lieu à Bâle (Suisse) du 29 mai au 5 juin 1954.

Pendant la semaine du Congrès, probablement 5 jours seront réservés aux discussions et 2 jours aux excursions. Avant et après le Congrès (25–28 mai et 7–19 juin) des excursions sont prévues pour faire connaître aux congressistes l'avifaune suisse, avant tout celle des Alpes et Préalpes. L'organisation du Congrès est confié au Secrétaire général, le professeur A. PORTMANN, Bâle.

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